Identifying seaweed consumption by sheep using isotope analysis of their bones and teeth: Modern reference $\delta^{13}C$ and $\delta^{15}N$ values and their archaeological implications

Magdalena Blanz[a,b,*], Ingrid Mainland[a], Michael Richards[c], Marie Balasse[d], Philippa Ascough[e], Jesse Wolfhagen[f,g], Mark A. Taggart[h], Jörg Feldmann[b]

[a]Archaeology Institute, University of the Highlands and Islands, Orkney College UHI, Kirkwall, Orkney, KW15 1LX, Scotland, UK
[b]Trace Element Speciation Laboratory (TESLA), Department of Chemistry, University of Aberdeen, Meston Building, Meston Walk, Aberdeen, AB24 3UE, Scotland, UK
[c]Simon Fraser University, Department of Archaeology, Burnaby, B.C, V5A 1S6, Canada
[d]UMR 7209 Archéozoologie, archéobotanique: sociétés, pratiques, environnements, CNRS/MNHN, 55 rue Buffon, 75005 Paris, France
[e]NERC Radiocarbon Facility, Scottish Universities Environmental Research Centre, Rankine Avenue, Scottish Enterprise Technology Park, East Kilbride G75 0QF, UK
[f]Department of Anthropology, Stony Brook University, Stony Brook, New York
[g]Department of Archaeology, Max Planck Institute for the Science of Human History, Kahlaische Straße 10, 07745 Jena, Germany
[h]Environmental Research Institute, University of the Highlands and Islands, Castle St, Thurso, Scotland, KW17 7JD, UK

*Corresponding author: m.blanz.11@aberdeen.ac.uk

This manuscript was accepted for publication in the Journal of Archaeological Science on 23rd March 2020.

Abstract

Seaweed consumption by wild, feral and domesticated animals in coastal areas world-wide is currently likely widely underestimated. Seaweed consumption on the Orkney Islands by domesticated animals has become an established part of the archaeological literature, but the extent of seaweed consumption elsewhere is still largely unknown in archaeological contexts. The identification of small amounts of seaweed consumption by collagen $\delta^{13}C$ and $\delta^{15}N$ values remains problematic, as it is unclear to what extent seaweed consumption is reflected in skeletal tissues, and how results may vary between different tissues.

In this study, modern sheep consuming known seaweed (predominantly kelp) and terrestrial diets on the Orkney Islands were analysed for $\delta^{13}C_{collagen}$, $\delta^{15}N_{collagen}$, $\delta^{13}C_{bone\ apatite}$ and $\delta^{13}C_{enamel}$ to provide a reference for archaeological studies. Seaweed and terrestrial vegetation were also analysed for $\delta^{13}C$ and $\delta^{15}N$ (n = 122). Seaweed $\delta^{15}N$ values did not differ significantly from terrestrial vegetation on North Ronaldsay, indicating that $\delta^{15}N$ is not a reliable indicator of seaweed consumption. In contrast, we confirmed that $\delta^{13}C$ is a suitable marker for substantial seaweed consumption in all studied tissues in herbivorous diets in the absence of C4 plants. The consumption of both seaweed and terrestrial vegetation led, to a large degree of variability in $\delta^{13}C$ results (−19.1 to −11.5 ‰) within one herd kept under a consistent management system, due to differences in the amount of seaweed consumed by the individual sheep. However, when only small amounts of seaweed are consumed (<25 %), this may not be evident in the $\delta^{13}C_{collagen}$ data. In contrast, when seaweed-consumption occurs primarily in winter, spring-born lambs may be expected to have substantially higher $\delta^{13}C$ values than their mothers. This study emphasises the need for modern reference data in archaeology, and may aid the identification of seaweed consumption by herbivores globally.

Keywords:
stable carbon isotopes ($\delta^{13}C$)
stable nitrogen isotopes ($\delta^{15}N$)
palaeodietary modelling
seaweed-eating sheep
prehistoric husbandry
dairying
seaweed stagger

1 Introduction

1.1 Seaweed-consumption

Seaweed is naturally consumed by wild and feral terrestrial mammals (e.g. deer, hares, pigs, coyotes) around the world to an extent that appears to be widely underestimated (Carlton and Hodder, 2003; Chimera et al., 1995; Conradt, 2000; Moore, 2004, 2002; Rose and Polis, 1998). In temperate climates, seaweeds are consumed particularly in winter and early spring when terrestrial resources are less abundant (Bay-Larsen et al., 2018), while in hotter climates, seaweed are eaten to survive dry summers (Moore, 2002). But seaweeds are also consumed when terrestrial resources are abundant (possibly related to their high iodine content; Moore, 2002; Stephenson, 1968). The consumption of seaweed by terrestrial mammals should thus be considered as a possibility in coastal areas around the world. Particularly in the North-West of Europe, seaweed is already known to have been consumed by, and fed to domesticated animals including sheep, cattle and pigs both today and historically (Bell, 1981; Fenton, 1997; Martin, 1716; Towsey, 2002). Additionally, stable carbon isotope ratio measurements on sheep's teeth and bones from the Orkney Islands, Scotland, have provided the first archaeological evidence of seaweed consumption by sheep, with earliest evidence from the Neolithic onward (around 3000 BC; Balasse et al., 2019, 2005; Dockrill et al., 1994). However, references to seaweed consumption by domesticated animals outside of Orkney are rare in the archaeological literature. This may be due to a lack of awareness of seaweed as a potential food source (Bell, 1981), or its (mistaken) dismissal as not applicable outside of Orkney, but crucially could also be caused by unfounded expectations of how seaweed consumption would be reflected in stable isotope ratios in consumer skeletal tissues (Balasse et al., 2019).

Seaweed species most commonly consumed by livestock generally have $\delta^{13}C$ values between −21 ‰ and −13 ‰ (Hansen et al., 2003a; Raven et al., 2002), while terrestrial C_3 plant material have lower $\delta^{13}C$ values (generally between −32 ‰ and −23 ‰, Kohn, 2010) and C_4 plant material higher $\delta^{13}C$ values (around −10 to −16 ‰, Basu et al., 2015; O'Leary, 1988). These dietary isotope ratios are passed on to consumers with an offset (the size of which differs between tissues and the composition of the diet), so that $\delta^{13}C$ values in consumer tissues, e.g. bones and teeth, can be used to infer past diets. In areas where C_4 plants were virtually absent, elevated consumer $\delta^{13}C$ values indicate marine food consumption (Chisholm et al., 1982). This includes the consumption of marine animals (fish, molluscs, seabirds etc.), but in the case of sheep these appear to be less accessible and less attractive than seaweed (Moore, 2002, although see also Steel, 1975). On Orkney, past seaweed consumption by sheep has primarily been identified by analysis of $\delta^{13}C$ in sequentially sampled tooth enamel, based on a modern reference dataset of seaweed-eating sheep (Balasse et al., 2009, 2005). However, in general, the analysis of bone collagen $\delta^{13}C$ and $\delta^{15}N$ values is currently much more common in archaeology. Currently we are aware of only two modern seaweed-eating sheep that have been analysed for bone collagen $\delta^{13}C$ (Ambers, 1990), and none for $\delta^{15}N$, so that interpretations of archaeological bone collagen $\delta^{13}C$ and $\delta^{15}N$ values have largely been based on assumptions as to how seaweed consumption would affect bone collagen. Additionally, studies at archaeological sites on Orkney have also resulted in seemingly conflicting evidence arising from $\delta^{13}C$ in bones compared to teeth (Schulting et al., 2017). Therefore, an analysis of how seaweed-consumption is reflected in bone collagen would be beneficial. The main aim of this paper is to provide a modern reference dataset of $\delta^{13}C$ in bone collagen, bone apatite and enamel, and of $\delta^{15}N$ in bone collagen of sheep consuming diets ranging from fully terrestrial to solely seaweed-eating, underpinned by analysis of

the consumed vegetation, to facilitate the interpretation of results from (potential) seaweed-eaters, and to discuss how seaweed consumption can be identified globally.

1.2 Background

Enamel and bone collagen $\delta^{13}C$ values each reflect different dietary components and periods of life. Bone collagen $\delta^{13}C$ values are influenced primarily by dietary protein consumed during or shortly before the period of bone formation or remodelling later in life, resulting in dietary averaging of several years (Froehle et al., 2010; Matsubayashi and Tayasu, 2019; Richards and Hedges, 1999; Webb et al., 2017). In contrast, enamel $\delta^{13}C$ values reflect the entire diet, but only for a short span during the early years of life, as this tissue is laid down over a short interval, and is not remodelled (Balasse, 2002; Zazzo et al., 2010). Through sequential sampling along the length of a tooth, a time-resolved record of the sheep's dietary $\delta^{13}C$ values while the tooth was growing can thus be obtained. This enables the identification of seasonal seaweed consumption (Balasse et al., 2005). However, the relationship between isotope ratios in these bones and teeth has never been studied directly in seaweed-eating sheep. This has given rise to some uncertainty within the archaeological literature with regard to how seemingly conflicting data from bones and teeth should be interpreted.

For example, sequential enamel measurements indicated substantial seasonal consumption of seaweed in winter months by all 11 adult sheep analysed at the Neolithic site of Holm of Papa Westray North Cairn, Orkney (with *c.* 44-69 % of dietary carbon during the cold season coming from seaweed; Balasse et al., 2006 and Balasse and Tresset, 2009). This indicates a herding strategy involving seaweed consumption over the course of multiple years and would be expected to be associated with elevated $\delta^{13}C_{collagen}$ values. However, the only two adult sheep from the same site (albeit likely different individuals to those analysed for $\delta^{13}C_{enamel}$) that were analysed for $\delta^{13}C_{collagen}$ did not show evidence of seaweed consumption (−19.8 ‰ and −20.1 ‰; Schulting and Richards, 2009). A similar discrepancy between enamel and bone $\delta^{13}C$ results at site level was found at Skara Brae, where sheep collagen $\delta^{13}C$ results were comparatively low (−21.1 ‰ to −20.3 ‰; Jones and Mulville, 2016), yet sequential tooth enamel $\delta^{13}C$ analyses indicated substantial seasonal seaweed consumption (Balasse et al., 2019). Similarly, at the Knap of Howar, recent reinterpretation of sequential $\delta^{13}C_{enamel}$ results indicates seasonal seaweed consumption in small amounts by some sheep (Balasse et al., 2019, 2006), while $\delta^{13}C_{collagen}$ results (potentially performed on different sheep; ranging from −20.7 ‰ to −18.8 ‰) have been interpreted as not being indicative of seaweed consumption (Bronk Ramsey et al., 2002; Schulting and Richards, 2009). In contrast, distinctly marine-influenced $\delta^{13}C_{collagen}$ values (−18.6 ‰ to around –13 ‰) have been found in five young lambs from Holm of Papa Westray North Cairn and Neolithic Quanterness, Orkney (Bronk Ramsey et al., 2009, 2002; Schulting et al., 2004, 2017; Schulting and Richards, 2009), whereas $\delta^{13}C_{collagen}$ of older sheep from the same sites did not clearly indicate a marine influence (Schulting and Richards, 2009). Schulting et al. (2017) suggest that this appears inconsistent as the lambs' values are dependent on the diets of their adult mothers as a result of gestation and nursing.

Part of the uncertainty regarding $\delta^{13}C_{collagen}$ values is caused by strong seasonal variability in the amount and digestibility of protein in seaweed as compared to grass (Applegate and Gray, 1995; Gaillard et al., 2018; Greenwood et al., 1983; Hansen et al., 2003a). If the seaweed component of a diet contained substantially lower amounts of digestible protein, $\delta^{13}C_{collagen}$ values would

disproportionately reflect grass in a mixed grass-seaweed diet (and vice versa), while $\delta^{13}C_{apatite}$ would be affected less by this difference in dietary protein. The offset between whole diet and collagen has also been shown to vary with protein origin (Froehle et al., 2010; Webb et al., 2017), indicating that simple mixing models are not sufficient to convert $\delta^{13}C_{collagen}$ values to a seaweed consumption percentage without more detailed prior knowledge of how seaweed consumption affects collagen isotope ratios, and the proportion of terrestrial and marine protein intake in a mixed diet. By consuming seaweed-eating sheep or their milk, a 'marine' isotopic signal can also be introduced to humans without direct exploitation of marine resources (Schulting and Richards, 2009), which could lead to apparently irreconcilable differences in isotope ratios and archaeological faunal assemblages. In addition to improving our understanding of husbandry practices (e.g. overwintering stock) and adaptations to the local environment, the study of domestic animal diets is therefore also required to research past human diets.

Nitrogen isotope ratios are a common complement to $\delta^{13}C_{collagen}$ measurements. Consumer $\delta^{15}N_{collagen}$ track dietary $\delta^{15}N_{protein}$ with an offset of ca. + 3-5 ‰, so that $\delta^{15}N$ data are mostly used to distinguish between trophic levels (O'Connell et al., 2012; Schoeninger et al., 1983; Webb et al., 2016). With respect to herbivores, elevated $\delta^{15}N$ has been considered as indicators of seaweed consumption (Jones and Mulville, 2016; Schulting et al., 2017). However, $\delta^{15}N$ in plants is affected by various environmental factors, including rainfall, mean annual temperature, local geology and the use of fertilisers, and varies seasonally (Craine et al., 2009). This necessitates further study into whether seaweeds can generally be expected to have higher $\delta^{15}N$ values than terrestrial grasses, or if certain environmental factors could cause deviation from such an overall trend. Direct comparison of $\delta^{15}N$ between modern seaweeds and grasses might serve to clarify this. Similar work on $\delta^{13}C$ would also be beneficial in providing more accurate dietary information for estimations of the amount of consumed seaweed. However, burning of fossil fuels since the 1850s have lowered $\delta^{13}C$ of atmospheric CO_2 (and entire ecosystems) by around 1.5 ‰, so that direct comparisons between archaeological and modern data need take this fossil fuel effect into account (also called Suess effect, Ambrose et al., 1997; Keeling, 1979; McCarroll et al., 2009). Due to the time delay in equilibration processes between the atmosphere and the ocean, the oceanic fossil fuel effect can be smaller in a given area than the atmospheric fossil fuel effect (Eide et al., 2017; Olsen et al., 2006; Takahashi et al., 2000). Because of this, seaweeds may be affected less than grasses, complicating fossil fuel effect corrections for mixed diets.

1.3 Research questions

In this paper, we present $\delta^{13}C$ and $\delta^{15}N$ data for modern bone collagen from both seaweed and terrestrial feeding sheep and $\delta^{13}C$ data for bone apatite and sequential enamel samples, as well as for terrestrial vegetation and seaweed sampled throughout the year from the sheep's grazing pastures. These results are then linked to previously published sequential enamel results for the same sheep (Balasse et al., 2012, 2009)**,** which were averaged (taking seasonal variability and annual periodicity into account by also considering $\delta^{18}O$) for comparison to bone collagen and bone apatite values. With this dataset, several questions were addressed, including: 1) What are expected bone collagen $\delta^{13}C$ and $\delta^{15}N$ values for completely terrestrial and completely seaweed diets in modern sheep? 2) Can these data be used to infer the amount of seaweed consumed by sheep from

archaeological $\delta^{13}C$ and $\delta^{15}N$ data? 3) Is the difference between $\delta^{13}C$ values in different tissues (enamel, bone apatite and bone collagen) in each animal affected by the amount of seaweed and grass in its diet? 4) Why are significantly elevated $\delta^{13}C_{collagen}$ values mainly observed in lambs among Neolithic and Bronze Age Orkney sheep?

2 Materials and methods

2.1 Modern reference samples

2.1.1 Sheep

Mandibles from two breeds of modern Northern European short-tailed sheep that consumed known diets were collected in 2004 on the Scottish Orkney islands of Rousay, Holm of Aikerness (near Westray) and North Ronaldsay (see map in supplementary information). The sheep from Rousay (n = 19) were all from the same herd of Shetland crosses and slaughtered at the age of 18 months. These sheep consumed only terrestrial pasture at Breckan, Upper Hunclett, Cottafea and Hunclett Hill (all on Rousay), where vegetation samples were also taken (see section 2.1.2). The sheep from North Ronaldsay (n = 15) were of the North Ronaldsay breed and were kept on the seashore by means of a drystone dyke, and mainly consumed seaweed, but also had access to small amounts of unimproved maritime heath and indigenous grassland throughout the year. Lambing ewes were taken inland and consumed cultivated grass from ca. April to August, while rams were left on the shore year-round. The sheep from the Holm of Aikerness, Westray, were also of the North Ronaldsay breed (n = 9) and are assumed to have consumed a diet that consisted almost solely seaweed, as terrestrial vegetation is virtually absent on the island. Some of these sheep may also have spent significant amounts of time on other islands, consuming terrestrial C_3 vegetation. More detailed descriptions of these sheep are given in Balasse et al. 2009 and 2012, which also report $\delta^{13}C$ and $\delta^{18}O$ results for sequentially sampled enamel from the same sheep. Samples for bone collagen and bone apatite analysis were taken from the sheep's mandibular coronoid processes.

2.1.2 Vegetation

Terrestrial and marine vegetation samples were collected from Rousay and North Ronaldsay in 2004 from the areas where the sheep in this study were pastured. To account for seasonal variation, samples were taken in summer (June), autumn (October) and winter (December). On North Ronaldsay, the pastures at Bar of Ryasgeo, Burrian and Nouster Bay were freely accessible to the sheep while shore-grazing. Closed off from the shore, ewes and lambs were kept in the Twingness pasture in summer to prevent them from eating seaweed during lambing time and while nursing. Vegetation samples were taken of green grass leaves and stems and pooled from several plants at the same sample location. Samples of both stranded and attached seaweeds were taken from North Ronaldsay focusing on *Laminaria spp.*; n = 17 and *Fucus sp.* and *Palmaria palmata*; each n = 1). The prominence of *Laminaria spp.* among these samples reflects the sheep's staple food choice (since availability of *Palmaria palmata*, their preferred seaweed, was limited both for sampling and consumption; Hansen et al., 2003a, 2003b).

Table 1 *List of vegetation samples taken and analysed for $\delta^{13}C$ and $\delta^{15}N$; NPK denotes a fertiliser containing nitrogen, phosphorus and potassium; for more detail see supplementary material*

Island	Pastures	Shores	Dominant vegetation	Improvements	Seasons sampled	No. of samples
Rousay	Hunclett Hill		indigenous grassland, heather (*Calluna vulgaris*) and rushes	unfertilised, no reseeding	Summer Autumn	11
	Giord		mixed reseeded grasses and indigenous grassland	unfertilised, some reseeding	Summer Autumn	9
	Cottafea, Breckan and Upper Hunclett		cultivated grass species such as rye grass (*Lolium spp*.) and timothy (*Phleum pratense)*	NPK fertilised, reseeded	Summer Autumn Winter	33
North Ronaldsay	Twingness		cultivated grasses	No recent fertilisation, potentially fertilised with NPK in the past	Summer	15
	Bay of Ryasgeo, Burrian and Nouster Bay		maritime heath and indigenous grassland	Unfertilised, no reseeding	Summer Autumn Winter	35
		Twingness, Burrian and Nouster Bay	seaweeds, including kelps *Laminaria digitata* and *Laminaria hyperborea*	N/A	Summer Autumn Winter	19

2.2 Archaeological samples

Three sheep mandibles were obtained from each of the following archaeological sites on Orkney: Point of Cott (Neolithic), Mine Howe (Iron Age) and Earl's Bu (Norse/Viking). Samples of cortical bone were taken from each mandible for the analysis of $\delta^{13}C$ and $\delta^{15}N$ in bone collagen. Sequentially sampled enamel of second and third molars from the same nine sheep had previously been analysed for $\delta^{13}C$ and $\delta^{18}O$ (Balasse et al., 2009).

2.3 Methods

2.3.1 Stable isotope analyses

Vegetation samples were dried at 50 °C for 24 h, followed by freeze-drying for 48 h. Measurement of $\delta^{15}N$ was performed using a Thermo-Finnigan Flash elemental analyser coupled to a Delta XP mass spectrometer in the Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany. Analysis of $\delta^{13}C$ on the same samples, previously published in a summarised form (and shown here in full), was performed as reported in Balasse et al. (2009).Bone collagen was extracted following the methods outlined in Richards and Hedges (1999) with the addition of an ultrafiltration step (Brown et al., 1988). Collagen extracts were measured for their carbon and nitrogen isotope ratios using the same analytical equipment as for the vegetation samples. All analyses were performed in duplicate. Analytical errors were 0.1 ‰ (1σ) for $\delta^{13}C$ and 0.2 ‰ (1σ) for $\delta^{15}N$.

For bone apatite analysis, powdered bone samples from the sheep's mandibular coronoid processes were flushed with helium. Phosphoric acid (prepared for isotopic analysis according to Coplen et al.,

1983) was added to the samples, and the resulting CO_2 was analysed by Continuous Flow Isotope Ratio Mass Spectrometry (CF-IRMS) to measure $\delta^{13}C$ and $\delta^{18}O$. Analyses of $\delta^{13}C_{enamel}$ of second molars of four sheep from Rousay (ROU6, ROU7, ROU8 and ROU18, whose $\delta^{18}O$ values alone were published in Balasse et al., 2012) were performed as reported in Balasse et al. (2009, 2012), including enamel pre-treatment with 2-3 % NaOCl and 0.1 M acetic acid. To assess differences in $\delta^{13}C$ arising due to enamel pre-treatment, samples from ROU7, ROU8 and ROU18 were also analysed without pre-treatment.

2.3.2 Data treatment

Isotope ratios are reported as per mil (‰) deviations from the VPDB and AIR international standards for carbon and nitrogen, respectively, and without fossil fuel effect corrections for $\delta^{13}C$. Statistical significance of differences between results for different sample groups was assessed by either two-sample two-tailed t-tests, one-way ANOVAs followed by post-hoc Tukey tests, or two-way ANOVAs, using Minitab software (Minitab 18, Minitab Inc., USA). The statistical significance threshold was set at $\alpha = 0.05$.

To enable a comparison between bone collagen and apatite $\delta^{13}C$ values (measured in this study) and sequential sampling enamel apatite $\delta^{13}C$ values (initially presented in Balasse et al., 2009), enamel $\delta^{13}C$ and $\delta^{18}O$ data were modelled to calculate a corrected "annual average" for each tooth from the seasonally varying sequential enamel $\delta^{13}C$ values. Simple averages of sequential samples do not accurately describe annual dietary behaviour because sequential samples may only cover a portion of a seasonal cycle captured in a tooth's enamel. To correct for variability in the annual signal captured in each tooth, $\delta^{13}C_{enamel}$ values were modelled with a seasonal regression model (Stolwijk, et al. 1999; analogous to the four-parameter model from Balasse et al., 2012). This model describes how isotopic values are expected to vary around an "annualised" average value based on regular deviations based presumably on seasonal dietary variation.

$$\delta^{13}C(dist) \sim Normal(\mu_{\delta^{13}C}[dist], \sigma_{\delta^{13}C}) \quad (1)$$

$$\mu_{\delta^{13}C}[dist] = M_{\delta^{13}C} + \beta_1 * \sin\left(2\pi\left(\frac{dist}{\lambda}\right)\right) + \beta_2 * \cos\left(2\pi\left(\frac{dist}{\lambda}\right)\right) \quad (2)$$

The λ parameter describes the length of tooth covered by a full seasonal cycle, while $M_{\delta 13C}$ describes the average value of the $\delta^{13}C$ cycle and thus represents an "annualised average" for the tooth. To avoid overfitting that would produce unreasonably extreme parameter values, we fit the isotopic (enamel $\delta^{18}O$ and $\delta^{13}C$) data with a multilevel Bayesian model that estimates tooth-level seasonal regression parameters (Wolfhagen, 2019). Posterior estimates of $M_{\delta 13C}$ describe the "annualised average" of $\delta^{13}C_{enamel}$ values for each sheep's second molar. These $M_{\delta 13C}$ values approximate a $\delta^{13}C_{enamel}$ value that reflects an animal's diet while its tooth formed (for second molars, ca. 3–12 months old; Balasse, et al. 2012).

Spacings between collagen $\delta^{13}C$ and bioapatite $\delta^{13}C$ (from enamel or bone) values were calculated according to Equation 3.

$$\Delta^{13}C_{co\text{-}ap} = \delta^{13}C_{collagen} - \delta^{13}C_{apatite} \quad (3)$$

3 Results

3.1 Vegetation

The vegetation data (Fig.1 and supplementary material) indicate similar $\delta^{13}C$ values occur for terrestrial vegetation from Rousay (mean ± 1σ was −29.8 ± 1.5 ‰; range −32.6 ‰ to −26.4 ‰; n = 53) and North Ronaldsay (−30.6 ± 2.9 ‰; range −33.0 ‰ to −27.2 ‰; n = 50). These terrestrial vegetation $\delta^{13}C$ values are significantly lower than those for seaweed from North Ronaldsay (−17.4 ± 1.4 ‰; range −21.2 ‰ to −14.0 ‰; n = 20; $p < 0.0001$). Autumn terrestrial vegetation from Rousay had around 1 ‰ higher $\delta^{13}C$ values than summer vegetation from the same sites (statistically significant with two-way ANOVA results of $F(1, 58) = 8.92$, $p = 0.004$ for seasonal differences; see figure in supplementary information).

Measured $\delta^{15}N$ values were lowest for Rousay terrestrial vegetation (2.8 ± 1.8 ‰; range −0.8 ‰ to 7.6 ‰; n = 53), and highest for North Ronaldsay terrestrial vegetation (6.2 ± 2.9 ‰; range 1.7 ‰ to 15.4 ‰; n = 50), while seaweed samples from North Ronaldsay had $\delta^{15}N$ values averaging 5.9 ± 1.2 ‰ (range 4.2 ‰ to 8.3 ‰; n = 20). One-way ANOVA and Tukey post-hoc tests showed no significant difference in $\delta^{15}N$ between the seaweed and terrestrial samples from North Ronaldsay, but a significant difference between these and the terrestrial samples from Rousay (one-way ANOVA: $F(2, 119) = 34.3$, $p < 0.05$). When comparing the *Laminaria spp.* seaweed samples (Fig. 2), $\delta^{15}N$ values were found to be around 1.6 ‰ higher in autumn than in winter (statistically significant with two-sample t-test $t(6) = 3.14$, $p = 0.02$).

As shown in Fig. 3, the lowest $\delta^{15}N$ average terrestrial vegetation values on Rousay were observed for the pasture furthest from the sea (Hunclett Hill), while the two NPK fertilised fields had higher values. The lowest $\delta^{15}N$ terrestrial vegetation values on North Ronaldsay were measured for the only NPK fertilised inland site sampled on the island, Twingness (4.6 ± 1.4 ‰; range 1.6 ‰ to 6.6 ‰; n = 15).

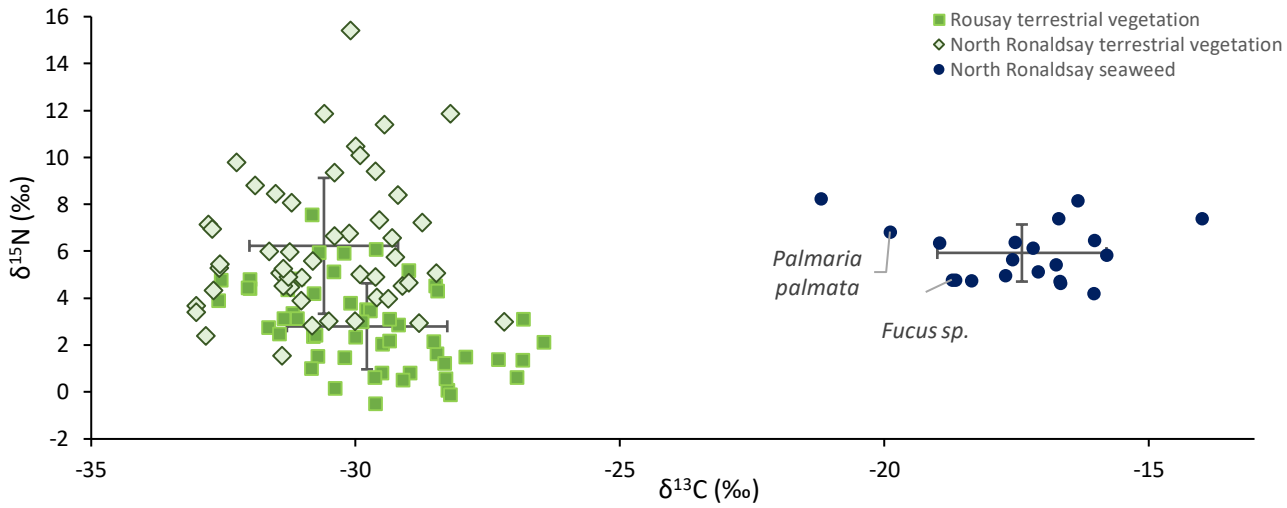

Fig. 1 *Vegetation $\delta^{13}C$ and $\delta^{15}N$ data for samples taken in autumn, summer and winter; the crosshairs indicate the mean ± 1σ for each vegetation group. All seaweed samples are* Laminaria spp.*, with the exception of the two data-points labelled otherwise. A summary of the $\delta^{13}C$ data was previously published in Balasse et al. 2009.*

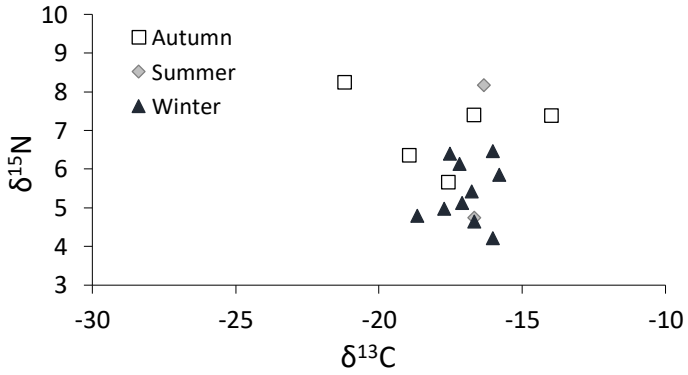

Fig. 2 *Vegetation $\delta^{13}C$ and $\delta^{15}N$ data for* Laminaria spp. *seaweeds from North Ronaldsay in summer, autumn and winter.*

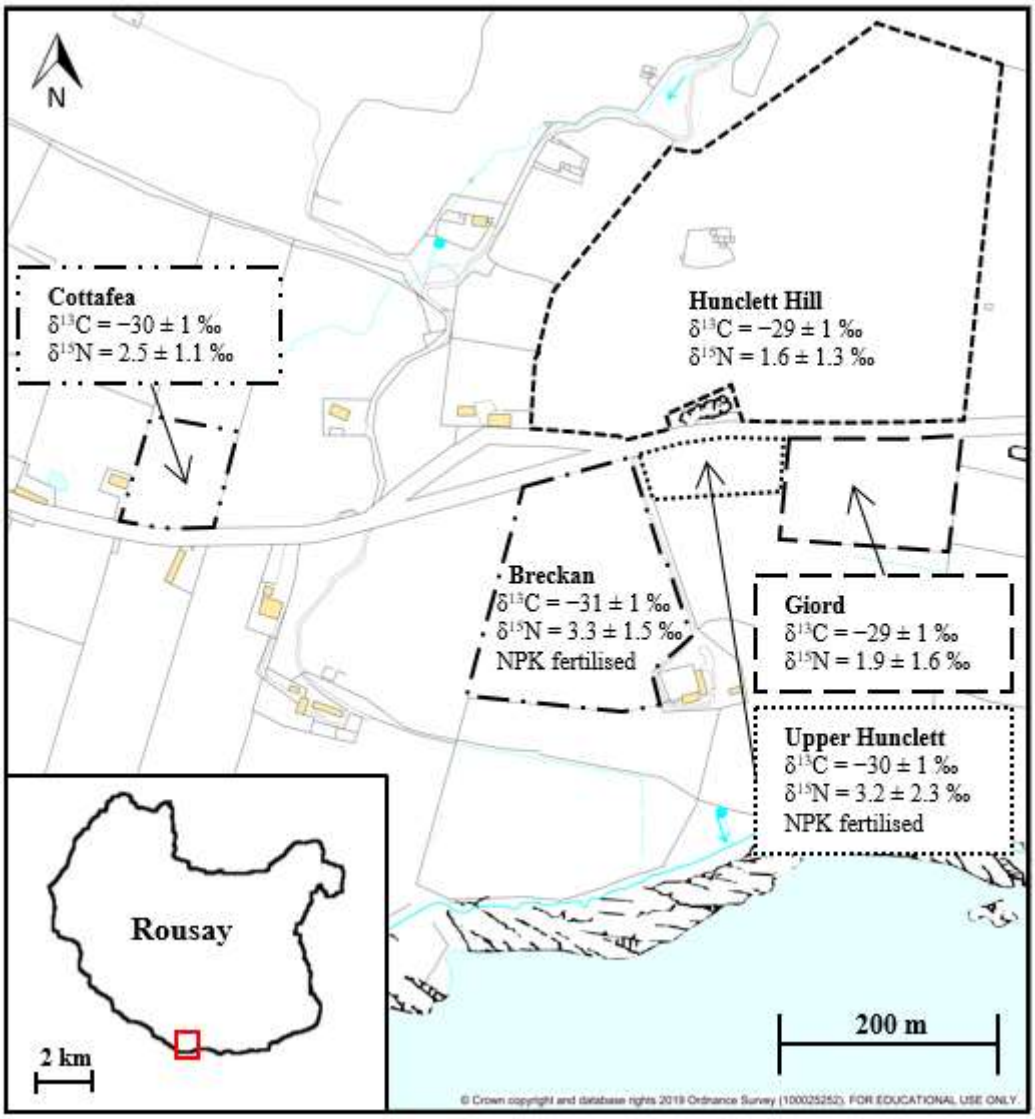

Fig. 3 *Map showing locations of Rousay pastures, average $\delta^{13}C$ and $\delta^{15}N$ data ± 1σ for autumn and summer vegetation samples, and fertilisation status (unfertilised if not stated otherwise). For Cottafae, only data for autumn samples are shown, as no samples were collected in summer. The box in the inset map of Rousay indicates the study area. Map modified from Digimap, © Crown copyright and database rights 2019 Ordnance Survey (100025252).*

3.2 Bone collagen

The results of the isotopic analyses of bone collagen are shown in Fig. 4 (and the supplementary material). A clear grouping of $\delta^{13}C$ values around −24.4 ‰ (1σ = 0.3 ‰) and $\delta^{15}N$ 7.4 ‰ (1σ = 0.4 ‰) is visible for terrestrial feeding sheep from Rousay, while the mainly seaweed-eating sheep from North Ronaldsay and the Holm of Aikerness (Westray) have more variable, but significantly higher $\delta^{13}C$ and $\delta^{15}N$ values (up to −10.7 ‰ and +10.4 ‰, respectively, for adult sheep, and $\delta^{15}N$ values of up to 12.7 ‰ for two 1-4 month-old lambs). Three of the sheep from Holm of Aikerness likely consumed terrestrial vegetation off-island, which is also supported by sequential tooth enamel results (see supplementary information – they will be referred to as exogenous sheep). The North Ronaldsay sheep with the lowest $\delta^{13}C$ value (−19.9 ‰) indicating increased grass consumption is

female, which is consistent with the herding strategy of keeping lambing ewes on terrestrial diets during the summer months. For the grass-eating Rousay sheep, the average trophic level increase observed was 4.6 ‰ for $\delta^{15}N$, and 5.3 ‰ for $\delta^{13}C$ (calculated by subtracting the average vegetation values from the average collagen values), while for seaweed-eating sheep from the Holm of Aikerness, the average trophic level increase was 3.6 ‰ for $\delta^{15}N$, and 6.1 ‰ for $\delta^{13}C$ (calculated as above, but excluding exogenous sheep with $\delta^{13}C$ values lower than −12 ‰, and lambs due to inherent additional trophic level effects from the consumption of milk).

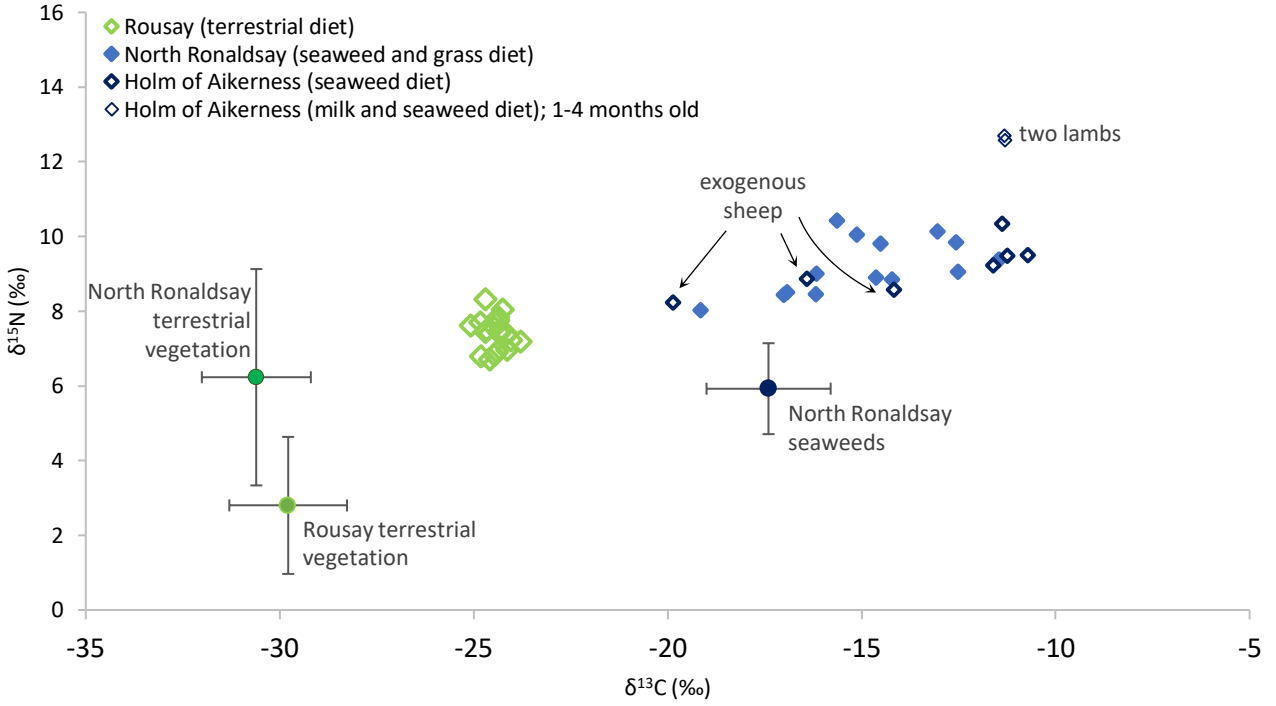

Fig. 4 *Graph of bone collagen $\delta^{13}C$ and $\delta^{15}N$ values of modern sheep mandibles, and means of vegetation samples, with error bars indicating ± 1σ.*

3.3 Apatite and $\Delta^{13}C_{co\text{-}ap}$

Bone apatite results and the annualised average results from the sequential enamel analysis in Balasse et al. (2009) and this study are shown in Fig. 5. Both the bone apatite and the annualised average enamel results show linear correlations with bone collagen results, though with different slopes. Only eleven sheep were analysed for enamel, bone apatite and bone collagen $\delta^{13}C$, while the others were sampled either for enamel or bone apatite in addition to bone collagen.

The calculations of $\Delta^{13}C_{co\text{-}ap}$ (i.e. spacing between bone collagen and apatite $\delta^{13}C$ values; Equation 3) indicate that $\Delta^{13}C_{co\text{-}ap}$ increases with increasing contribution of seaweed to the diet when considering bone apatite (Fig. 5 and supplementary material). No such linear trend is observable between the enamel $\Delta^{13}C_{co\text{-}ap}$ spacing and $\delta^{13}C_{collagen}$ (Fig. 5).

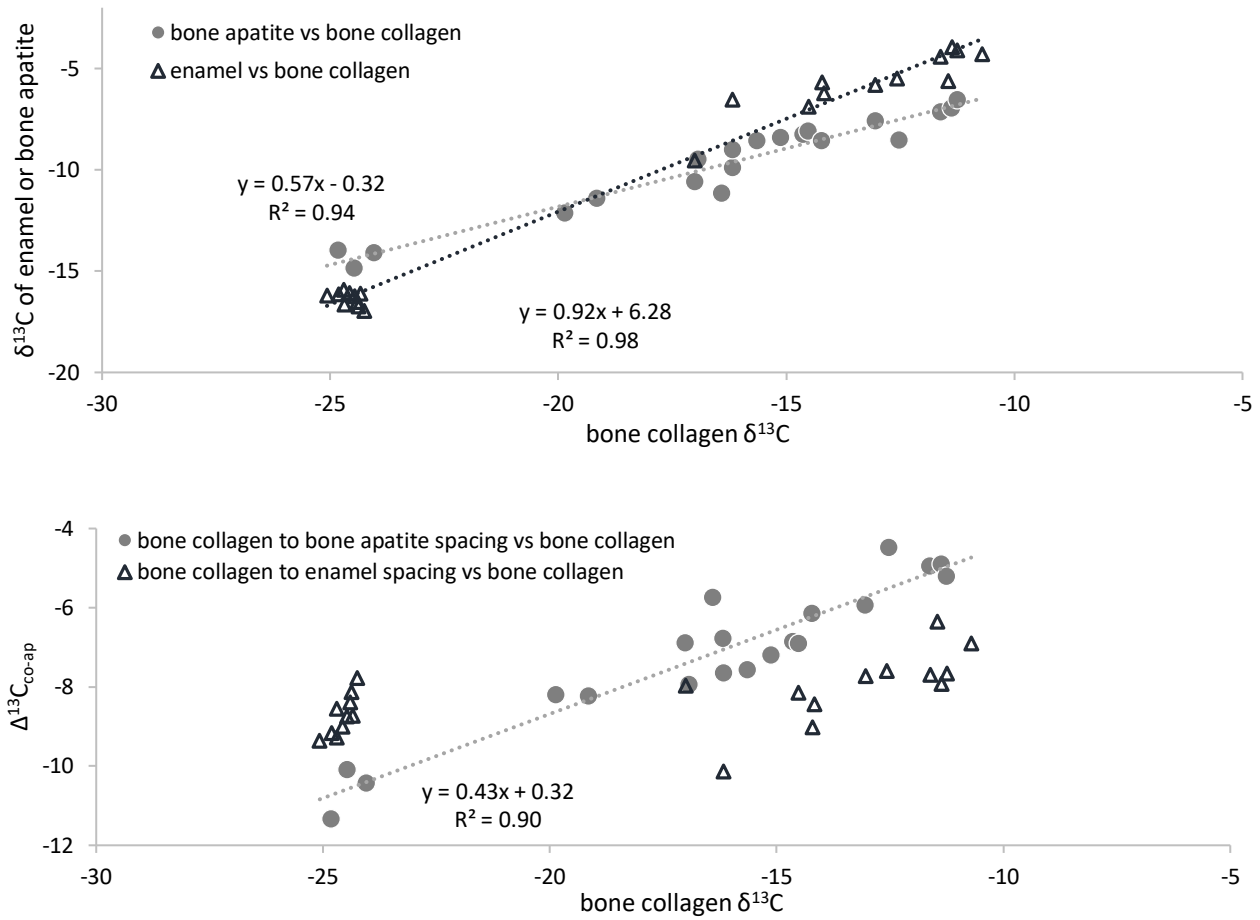

Fig. 5 Top: *Graph of $\delta^{13}C$ of enamel or bone apatite vs $\delta^{13}C_{collagen}$, indicating largely linear correlations with differing slopes; each symbol gives $\delta^{13}C$ results for one animal; enamel results are annualised averages;* Bottom: *Graph of $\Delta^{13}C_{co\text{-}ap}$ (spacing between bone collagen and bone or enamel apatite, see Equation 3) plotted against $\delta^{13}C_{collagen}$; one trendline omitted due to lack of linear correlation*.

3.4 Archaeological material

Displayed in Fig. 6, the sampled archaeological sheep had $\delta^{13}C_{collagen}$ values ranging from −22.9 ‰ to −20.4 ‰ (−21.5 ± 0.9 ‰; mean ± 1σ), with the exception of one sheep from the Neolithic site of Point of Cott, which had a $\delta^{13}C_{collagen}$ value of −18.1 ‰ (for comparison, add +1.5 ‰ to the modern data due to the fossil fuel effect; but see section 4.2). The $\delta^{15}N$ values ranged from 5.7 to 9.1 ‰.

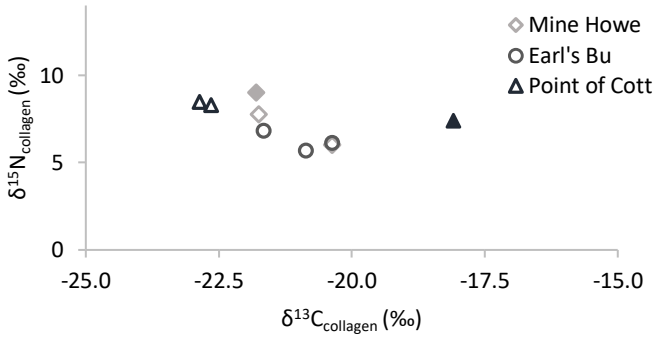

Fig. 6 *Graph of bone collagen $\delta^{13}C$ and $\delta^{15}N$ values of the archaeological sheep mandibles; filled symbols indicate individuals with elevated $\delta^{13}C_{enamel}$ values indicative of seaweed consumption, while empty symbols indicate sheep where no clear evidence of seaweed-consumption was present in $\delta^{13}C_{enamel}$, as reported in Balasse et al. (2009). Data not adjusted for the fossil fuel effect.*

4 Discussion

4.1 Nitrogen Isotope ratios, $\delta^{15}N$

4.1.1 Vegetation

Seaweed $\delta^{15}N$ values are generally assumed to be higher than those of terrestrial grasses (e.g. Gigleux et al., 2017; Jones and Mulville, 2016; Mays and Beavan, 2012; Schulting et al., 2017). In contrast to this, the unimproved coastal grasslands on North Ronaldsay had $\delta^{15}N$ values very similar to those of seaweed from the same island, while Rousay terrestrial vegetation had ∼3 ‰ lower $\delta^{15}N$ values, similar in magnitude to one trophic level difference (Fig. 1).

This difference between North Ronaldsay and Rousay terrestrial vegetation $\delta^{15}N$ is likely not due to differences in environmental factors as these islands are within 50 km of each other and have the same underlying geology (Astin, 1990). While the use of modern NPK fertilisers can lower $\delta^{15}N$ values (Bateman and Kelly, 2007; Blanz et al., 2019), the samples here from NPK fertilised pastures on Rousay had higher $\delta^{15}N$ values than nearby unfertilised pastures. Salt spray can also lead to elevated $\delta^{15}N$ values (Heaton, 1987; Virginia and Delwiche, 1982), which may fit this dataset (with respect to relative distance of each sampling area to the sea on each island; Fig. 3), but likely does not fully account for the differences seen in terrestrial vegetation $\delta^{15}N$ values between the islands.

Another contributing factor here may be the sheep's dung, as animal dung fertilisation can lead to elevated $\delta^{15}N$ values (e.g. Bogaard et al., 2007; Bol et al., 2005; Fraser et al., 2011; Styring et al., 2014). Since sheep on the shores of North Ronaldsay primarily consume seaweed, which has elevated $\delta^{15}N$ values compared to, e.g., the grass samples from Rousay, their dung $\delta^{15}N$ values are likely additionally elevated. The stocking density on North Ronaldsay is also relatively high, with ∼12 sheep per hectare when the tide is in, and 5 sheep per hectare when the tide is out (K. Woodbridge,

personal communication, 2019, and Hall, 1975), compared to only ~3 sheep per hectare for the reference herd in Rousay. Following this, the (inadvertent) intensive fertilisation with high $\delta^{15}N$ dung by the mainly seaweed-eating sheep, perhaps combined with a sea spray effect, is suggested as the source of elevated $\delta^{15}N$ values in the North Ronaldsay terrestrial vegetation on the shore side of the sheep dyke. This interpretation is also supported by the lower $\delta^{15}N$ values in grass from the inland pasture of Twingness (North Ronaldsay), which is not available to the shore-grazing sheep.
Seaweed $\delta^{15}N$ values in temperate climates appear to be lower in winter and spring than in autumn and late summer by ~2-5 ‰ (Carvalho et al., 2008; Lemesle et al., 2015; this study). Since the consumption of seaweed by sheep appears to be highest in winter and early spring when stranded seaweed is more abundant due to storms and grass becomes scarce (Balasse et al., 2006; Chapman, 1970; Hansen et al., 2003a; Martin, 1716; Ryder, 1983), these seasonally lower $\delta^{15}N$ values should be taken into account when interpreting and modelling $\delta^{15}N$ values of seaweed consumers.

4.1.2 $\delta^{15}N$ for evaluating the amount of dietary seaweed

The seaweed-eating sheep from North Ronaldsay and Holm of Aikerness had elevated $\delta^{15}N$ values compared to the grass-eating sheep from Rousay (Fig. 4). However, since the terrestrial vegetation on North Ronaldsay also had elevated $\delta^{13}C$ values, a sheep consuming only grass on the coast of North Ronaldsay may be expected to have similarly elevated $\delta^{15}N$ values. Considering the various factors that can lead to elevated $\delta^{15}N_{collagen}$ values, which include the consumption of dung- or seaweed-fertilised crops (Blanz et al., 2019; Bogaard et al., 2007) and vegetation affected by salt spray or consumed on saltmarshes (Britton et al., 2008; Heaton, 1987; Virginia and Delwiche, 1982), age effects (Webb et al., 2016) and trophic level effects through the consumption of milk (Fogel et al., 1989) and even seabirds (Furness, 1988; Steel, 1975) and fish offal (Ryder, 1983), elevated $\delta^{15}N_{collagen}$ does not appear to be a reliable marker for the consumption of seaweed. While in the absence of the above food groups, seaweed does appear to have slightly elevated mean $\delta^{15}N$ values compared to terrestrial grass, this is not certain at any given site. The North Ronaldsay terrestrial vegetation data in this study may be somewhat atypical due to intensive fertilisation with seaweed-eating sheep dung; however, Stevens et al. (2006) also showed that deer that were most likely consuming seaweed did not have elevated $\delta^{15}N_{collagen}$ values. Similarly, the archaeological sheep from Point of Cott that shows evidence of seaweed consumption in $\delta^{13}C_{collagen}$ did not have elevated $\delta^{15}N$ values compared to the sheep that did not show evidence of seaweed consumption (Fig. 6). This may also be related to recent findings that $\delta^{15}N$ values have low sensitivity to small amounts of marine consumption (Webb et al., 2016). Therefore, while consumption of seaweed may cause elevated $\delta^{15}N_{collagen}$ values if alternative food sources have substantially lower $\delta^{15}N$ values (e.g. in Hansen et al., 2019), this is not always the case, and it should not be assumed that seaweed consumption automatically causes elevated $\delta^{15}N_{collagen}$. Likewise, elevated $\delta^{15}N_{collagen}$ values are not diagnostic of the consumption of seaweed.

4.2 Stable carbon isotope ratios, $\delta^{13}C$

The substantial seaweed-consumption by sheep on North Ronaldsay and the Holm of Aikerness is clearly reflected in their $\delta^{13}C_{collagen}$ and $\delta^{13}C_{apatite}$ values (Fig. 4 and supplementary information). Three sheep from Holm of Aikerness had $\delta^{13}C_{collagen}$ values lower than −14 ‰, which is inconsistent with

the sole consumption of seaweed (virtually the only food available on the Holm of Aikerness) throughout the year. However, occasionally sheep are moved onto the island, for example importing of rams to reduce inbreeding, and the collecting and returning bottle-fed orphaned lambs (Balasse et al., 2009 and Una Gordon 2019, pers. comm.). The sheep with lower $\delta^{13}C_{collagen}$ values on Holm of Aikerness thus likely spent some time off the island, consuming milk and/or terrestrial C_3 vegetation, and should be excluded when considering solely seaweed-eating sheep.

The difference between average $\delta^{13}C_{collagen}$ values from solely terrestrial-eating sheep (–24.4 ± 0.3 ‰) and seaweed-eating sheep (–11.2 ± 0.3 ‰), is large when compared to other studies. For example, Richards and Hedges (1999) noted an average $\delta^{13}C_{collagen}$ difference of ~8 ‰ between completely terrestrial and completely marine diets in human bones. However, in an archaeological context, the $\delta^{13}C_{collagen}$ difference between completely terrestrial- and completely seaweed-eating sheep $\delta^{13}C$ values can be expected to be slightly smaller than that reported for the modern animals in this study due to the smaller magnitude of the oceanic fossil fuel effect compared to the atmospheric fossil fuel effect (Eide et al., 2017; Olsen et al., 2006; Takahashi et al., 2000). But even taking this potential difference into account, the $\delta^{13}C_{collagen}$ range from solely terrestrial-eating sheep (C_3-plants) and kelp-eating sheep in archaeological contexts can still be expected to span over 11 ‰.

4.2.1 Vegetation and herd variability

On Rousay, the seasonal differences in $\delta^{13}C$ of terrestrial grassland and maritime heath, as well as variation between neighbouring pastures, were found to be relatively low (Figs. 1 and 3), as was the variation in $\delta^{13}_{collagen}$ values (range of 1.3 ‰; 1σ = 0.3 ‰). In contrast, the range of $\delta^{13}C_{collagen}$ values was much larger among North Ronaldsay sheep (range of 7.6 ‰, Fig. 4), despite also using one consistent management system (albeit one that differentiates between rams and ewes). This variation most likely reflects differences in the extent to which sheep consumed grass and seaweed (as well as which species and seaweed parts were consumed). Importantly, this large amount of variation in the North Ronaldsay sheep indicates that significant differences in $\delta^{13}C$ values between individual sheep cannot always be taken as evidence of significant differences in sheep management (or sheep origin), particularly when considering only small numbers of archaeological animals.

4.2.2 Tissue differences in $\delta^{13}C$

Despite bone collagen $\delta^{13}C$ primarily being influenced by dietary protein (Webb et al., 2017), whereas bone apatite $\delta^{13}C$ is affected by the entire diet (Froehle et al., 2010; Kellner and Schoeninger, 2007), the bone apatite $\delta^{13}C$ and collagen $\delta^{13}C$ values for the sheep in this study (Fig. 5, top) correlate linearly. This indicates that $\delta^{13}C_{collagen}$ in the adult sheep consuming mixed diets containing significant amounts of both grass and seaweed is not substantially biased toward either seaweed or grass consumption compared to the $\delta^{13}C_{apatite}$ values. Unfortunately, the effects of consuming only small amounts of seaweed as part of largely terrestrial diets on $\delta^{13}C_{collagen}$ as compared to $\delta^{13}C_{enamel}$ are still unclear due to a lack of modern samples.

One example of seemingly conflicting collagen and enamel $\delta^{13}C$ results is given by sheep MH02 (age at death 4-8 years) from the Iron Age site Mine Howe (Fig. 6), which had $\delta^{13}C_{enamel}$ indicative of seasonal seaweed consumption in the winter of the sheep's second year (ranging from −12.5 ‰ to −8.4 ‰ in a third molar; Balasse et al., 2009). However, its $\delta^{13}C_{collagen}$ value (−21.8 ‰) was similar to

other sheep at the site whose enamel did not show evidence of seaweed consumption. If seaweed consumption by this sheep was limited to the one winter represented in the enamel, this might be due to dietary averaging in bone and bone turnover over the 4-8 year life period of this sheep (although see Matsubayashi and Tayasu, 2019). However, taking these data together with the cases of Holm of Papa Westray North, Skara Brae and Knap of Howar described in the introduction, there is mounting evidence that small amounts of seasonal seaweed consumption may not be clearly apparent in $\delta^{13}C_{collagen}$ values from adult sheep (similar to Hedges' theoretical model that showed up to 30 % marine protein in diet may be missed when considering $\delta^{13}C_{collagen}$; Hedges, 2004), but is apparent when sequentially sampling enamel.

Since $\delta^{13}C_{collagen}$ values are biased toward dietary protein particularly in protein-rich diets (Webb et al., 2017), while $\delta^{13}C_{apatite}$ values reflect the whole diet (Froehle et al., 2010; Kellner and Schoeninger, 2007), and because of differing tissue formation processes and rates, constant spacing between collagen and apatite $\delta^{13}C$ values may not be assumed for different diets. Similar to the results presented in Fig. 5 (bottom), previous studies of North American and African herbivores also show linear trends in $\Delta^{13}C_{co\text{-}ap}$ spacing differences (Clementz et al., 2009; Codron et al., 2018). As sheep rumen microbiology has been shown to adapt to seaweed diets (Greenwood et al., 1983; Orpin et al., 1985), the extent of the dietary adaptation likely also affects seaweed digestibility, and thus tissue $\delta^{13}C$ values and spacings.

While differences in bioapatite pre-treatment can also affect $\delta^{13}C$ (Pellegrini and Snoeck, 2016), this does not appear to have given rise to the varying spacings observed here (see supplementary information). Instead, seasonal differences in bone formation rates may have affected the spacings: Sheep bones appear to increase in bone mass in summer, while greater resorption occurs in winter (Arens et al., 2007). Lower $\delta^{13}C_{enamel}$ values were recorded for Rousay sheep in enamel formed in winter compared to summer (Balasse et al., 2009), while seasonally seaweed-eating sheep from North Ronaldsay tended to have higher $\delta^{13}C_{enamel}$ in winter. If winter diets are underrepresented in bone, but not in enamel, this would cause elevated $\delta^{13}C_{bone\ apatite}$ compared to $\delta^{13}C_{enamel}$ for Rousay sheep, but lower $\delta^{13}C_{bone\ apatite}$ compared to $\delta^{13}C_{enamel}$ for North Ronaldsay sheep and may also explain discrepancies between $\delta^{13}C_{collagen}$ and $\delta^{13}C_{enamel}$.

4.2.3 Trophic level changes

The observed difference in $\delta^{13}C$ of around 5-6 ‰ between primary producers and adult sheep collagen is similar to that for previous work on herbivores (Krueger and Sullivan, 1984; Lee-Thorp et al., 1989; Vogel, 1978). Pigs fed with diets including varying amounts of marine protein also produced similarly high diet-collagen $\delta^{13}C$ offsets of 3-7 ‰ (Webb et al., 2017). In the same trial, 4-week-old piglets had only 0.5 ‰ higher $\delta^{13}C_{collagen}$ values than their sows when consuming sow-milk and the same feed as the sows. This is also largely similar to the data reported here from the sheep on Holm of Aikerness, where no significant difference in $\delta^{13}C$ was found between two lambs and four adult sheep with $\delta^{13}C > -12$ ‰, indicating that lamb $\delta^{13}C_{collagen}$ reflects the diet of their mothers shortly before, or during gestation and nursing (following a ewe-diet to collagen $\delta^{13}C$ offset of 5-6 ‰).

4.3 Lambs, seaweed and dairying

Schulting et al. (2017) suggested that the apparent predominance of $\delta^{13}C_{collagen}$ values indicative of seaweed diets in lambs compared to adult sheep at Holm of Papa Westray North and Quanterness indicates seaweed to be a fall back strategy when terrestrial resources have failed, since burial assemblages are biased by differential survivorship: As many of the animals showing evidence of maternal seaweed consumption in $\delta^{13}C_{collagen}$ died young, they argue that this may indicate seaweed was only being used as a last resort.

However, a general bias toward elevated $\delta^{13}C_{collagen}$ values in sheep younger than around two months compared to their mothers is to be expected when seaweed is primarily consumed during winter and lambing occurs in April to May (Balasse et al., 2017, 2006): Seasonal seaweed consumption by ewes is subject to dietary averaging in bones over multiple years, including the previous summers and autumns spent consuming grass (though this also depends on the sampled part of the bone; Matsubayashi and Tayasu, 2019). In contrast, lamb bone collagen at the age of 0-2 months is primarily formed from carbon passed on from the mother both before birth (in the womb), and after birth (in the form of milk). Therefore, seaweed consumption by the ewe during gestation and nursing (in winter and spring) will likely have a much larger effect on $\delta^{13}C_{collagen}$ of the lamb than the mother. Since nursing ewes feeding on seaweed have been reported from Norwegian coastal areas (where lambing begins in April, but extensive grass consumption can only begin in May; Ryder 1983), and for milking cows on the isle of Tiree (Scotland) that fattened on seaweed (Martin 1716), this scenario is not unlikely. The archaeological evidence of routine seasonal seaweed-consumption in adult sheep at Holm of Papa Westray North spans over multiple years indicating survival with this strategy. Since there are indications that seasonal seaweed consumption may not always be clearly apparent in adult sheep $\delta^{13}C_{collagen}$ values .the predominance of elevated $\delta^{13}C_{collagen}$ values in lambs (as compared to adult sheep) described by Schulting et al. (2017), may therefore, on balance, also be the result of a successful herding strategy involving regular seasonal seaweed-consumption over many years.

With respect to mortality profiles of burial assemblages, lamb mortality is not necessarily connected to starvation and a lack of terrestrial resources, but could also be due to deliberate killing of young animals, e.g. as part of dairy-herd management, or to the greater vulnerability of young lambs to illness, predators, and physical trauma caused by falls while running (Baker and Britt, 1990; Hewson, 1984; Houston, 1977). Another possibility is nutrient deficiency: It has been observed that when nursing ewes consume seaweed, their lambs may develop a neurological disorder (so-called 'seaweed stagger') due to copper deficiency (caused by low Cu bioavailability in seaweed), which can lead to considerable lamb mortality (Hallsson, 1964; Ingimundarson, 1995; Palsson and Girmsson, 1953). Until the middle of the last century, the reason behind this disorder was not understood. However, even before this some traditional herding practices incorporated knowledge that lambs and nursing ewes should be kept on grass, with a prime example being North Ronaldsay, where lambing ewes are traditionally taken from the shore to inland grass pastures every year (North Ronaldsay Native Sheep Regulations, 1902). Ethnographic evidence from Iceland also indicates that lambs suffering from seaweed stagger can (in some cases) be attributed to an '*inexperienced farmer who let his ewes eat too much seaweed*' (Ingimundarson, 1995, p. 95), as opposed to actual scarcity of terrestrial forage and fodder. While seaweed certainly gained in importance as an animal food source in winter and spring, sheep also voluntarily consume seaweed when other food sources are

available (Hall, 1975; Landsborough, 1857; Paterson and Coleman, 1982; own observations). If sheep were to 'overindulge' on such a diet, this may affect lamb mortality. Young dead lambs in the archaeological record with particularly marine $\delta^{13}C_{collagen}$ values may thus also be indicative of inexperience with the use of seaweed as a food (on the part of the herder), leading to misjudgements. Another possible interpretation is that sheep were left to freely roam on a coastal piece of land, withlittle further dietary management.

Additionally, young sheep seeming 'ill' (i.e. with seaweed stagger) may have been killed deliberately so that resources could be kept for healthier animals, also rendering ewe's milk available. The human use of sheep/goat milk is attested in the study area by ethnographic and historic evidence on the Shetland Islands, Faroe Islands and Iceland (Baldwin, 1978; Gifford, 1879; Martin, 1716; Ryder, 1983). Thus, if a milking economy was the aim, a conscious decision may have been made to keep ewes on seaweed during the lambing season (e.g. by foddering seaweed), as getting the ewes through the winter well while milking was perhaps seen as more important than the health of the lambs, which were to be killed soon after birth. There is currently no evidence available at Holm of Papa Westray North to support this particular theory, however. Nevertheless, seaweed can be a valuable resource as animal food and fodder, depending on its management and herding strategy, and its use alone should not be taken as evidence of terrestrial resource failure.

5 Conclusions

In presenting a reference dataset of $\delta^{13}C$ and $\delta^{15}N$ in modern grass- and seaweed-eating sheep (collagen and enamel), as well as consumed vegetation, this study gives insights into how seaweed consumption is reflected in skeletal tissues. The results indicate that $\delta^{15}N_{collagen}$ values are not particularly beneficial for the identification of seaweed-consumption, but $\delta^{13}C_{collagen}$ values should reliably reflect substantial seaweed consumption. When only smaller amounts of seaweed are consumed, this is less clear for $\delta^{13}C_{collagen}$ from adult animals. Further research is required, but it appears that small amounts of seasonal seaweed consumption are most apparent in lambs when studying $\delta^{13}C_{collagen}$, while routine measurements of collagen $\delta^{13}C$ and $\delta^{15}N$ may sometimes miss seasonal seaweed-consumption. However, sequential $\delta^{13}C_{enamel}$ results can display clearer evidence of seasonal seaweed consumption in adults. As also evidenced by others (e.g., Froehle et al., 2010; Webb et al., 2017), relying solely on bulk $\delta^{13}C_{collagen}$ appears to risk the loss of key dietary information, and seems prone to some misinterpretation. This is additionally compounded by a widespread lack of awareness of seaweed as a potential dietary source for terrestrial mammals Moore, 2002). Especially seasonal and low-level seaweed-consumption is therefore likely underrecognized in the global archaeological record, leading to underestimations of the contribution of marine resources being exploited world-wide, and misapprehensions of past coastal economies and animal husbandry practices. Therefore, the (pre)history of seaweed-consumption by both humans and animals is still largely unknown, as is the extent of the indirect contribution of seaweed to human dietary stable isotope ratios through consumption of meat or milk of seaweed-eating animals. The refinement, or development of further methods of identifying seaweed consumption is thus required.

6 Acknowledgments

This research was funded by the British Natural Environment Research Council (NERC; NER/B/S/2003/00223) and the European Social Fund and Scottish Funding Council as part of Developing Scotland's Workforce in the Scotland 2014-2020 European Structural and Investment Fund Programme. Stable isotope values in tooth enamel were measured at the SSMIM (Paris, MNHN) with technical support of Joël Ughetto. Modern sheep mandibles and/or information on sheep herding practices on Orkney were kindly provided by Robert Mainland (Rousay), Linda Hagan and Una Gordon (Holm of Aikerness), Billy Muir, Dr Kevin Woodbridge and the North Ronaldsay Sheep Court (North Ronaldsay). We would like to thank Anne Brundle, Tankerness House Museum, Orkney (Point of Cott), Dr Colleen Batey, University of Glasgow (Earl's Bu) and Prof Jane Downes and Nick Card, Orkney College, UHI (Mine Howe) for providing access to the archaeological mandibles. The authors would also like to thank Jane Outram and Mandy Jay for assistance in preparation and isotopic measurement of the vegetation samples, which were kindly collected by Robert Craigie, and Karen Chapman for preparing the mandibles. Lastly, the authors are also grateful for the constructive comments of the editors and anonymous reviewers.

Appendix: Supplementary Material

Supplementary material to this article is available online, or by contacting the authors.

References

Ambers, J.C., 1990. Identification of the use of marine plant material as animal fodder by stable isotope ratios. 'Proceedings Second Int. Symp. 14C Archaeol. 29, 251–258.

Ambrose, S.H., Butler, B.M., Hanson, D.B., Hunter-Anderson, R.L., Krueger, H.W., 1997. Stable isotopic analysis of human diet in the Marianas Archipelago, western Pacific. Am. J. Phys. Anthropol. 104, 343–361. https://doi.org/10.1002/(SICI)1096-8644(199711)104:3<343::AID-AJPA5>3.0.CO;2-W

Applegate, R.D., Gray, P.B., 1995. Nutritional value of seaweed to ruminants. Rangifer 15, 15–18. https://doi.org/10.7557/2.15.1.1152

Arens, D., Sigrist, I., Alini, M., Schawalder, P., Schneider, E., Egermann, M., 2007. Seasonal changes in bone metabolism in sheep. Vet. J. 174, 585–591. https://doi.org/10.1016/j.tvjl.2006.10.001

Astin, T.R., 1990. The Devonian lacustrine sediments of Orkney, Scotland; implications for climate cyclicity, basin structure and maturation history. J. Geol. Soc. London. 147, 141–151. https://doi.org/10.1144/gsjgs.147.1.0141

Baker, J.R., Britt, D.P., 1990. Causes of death in the native sheep of North Ronaldsay, Orkney. II. Lambs. Br. Vet. J. 146, 143–146. https://doi.org/10.1016/0007-1935(90)90006-O

Balasse, M., 2002. Reconstructing dietary and environmental history from enamel isotopic analysis: Time resolution of intra-tooth sequential sampling. Int. J. Osteoarchaeol. 12, 155–165. https://doi.org/10.1002/oa.601

Balasse, M., Mainland, I., Richards, M.P., 2009. Stable isotope evidence for seasonal consumption of marine seaweed by modern and archaeological sheep in the Orkney archipelago (Scotland). Environ. Archaeol. 14, 1–14. https://doi.org/10.1179/174963109X400637

Balasse, M., Obein, G., Ughetto-Monfrin, J., Mainland, I., 2012. Investigating seasonality and season of birth in past herds: A reference set of sheep enamel stable oxygen isotope ratios. Archaeometry 54, 349–368. https://doi.org/10.1111/j.1475-4754.2011.00624.x

Balasse, M., Tresset, A., Ambrose, S.H., 2006. Stable isotope evidence (δ13C, δ18O) for winter feeding on seaweed by Neolithic sheep of Scotland. J. Zool. 270, 170–176. https://doi.org/10.1111/j.1469-7998.2006.00104.x

Balasse, M., Tresset, A., Bălăşescu, A., Blaise, E., Tornero, C., Gandois, H., Fiorillo, D., Nyerges, E.A., Frémondeau, D., Banffy, E., Ivanova, M., 2017. Animal Board Invited Review: Sheep birth distribution in past herds: A review for prehistoric Europe (6th to 3rd millennia BC). Animal 11, 2229–2236. https://doi.org/10.1017/S1751731117001045

Balasse, M., Tresset, A., Dobney, K., Ambrose, S.H., 2005. The use of isotope ratios to test for seaweed eating in sheep. J. Zool. 266, 283–291. https://doi.org/10.1017/S0952836905006916

Balasse, M., Tresset, A., Obein, G., Fiorillo, D., Gandois, H., 2019. Seaweed-eating sheep and the adaptation of husbandry in Neolithic Orkney: new insights from Skara Brae. Antiquity 370, 919–932.

Baldwin, J.R., 1978. Norse influences in sheep husbandry on Foula, Shetland. Scand. Shetl. An Ongoing Tradit.

Basu, S., Agrawal, S., Sanyal, P., Mahato, P., Kumar, S., Sarkar, A., 2015. Carbon isotopic ratios of modern C3-C4 plants from the Gangetic Plain, India and its implications to paleovegetational reconstruction. Palaeogeogr. Palaeoclimatol. Palaeoecol. 440, 22–32. https://doi.org/10.1016/j.palaeo.2015.08.012

Bateman, A.S., Kelly, S.D., 2007. Fertilizer nitrogen isotope signatures. Isotopes Environ. Health Stud. 43, 237–247. https://doi.org/10.1080/10256010701550732

Bay-Larsen, I., Risvoll, C., Vestrum, I., Bjørkhaug, H., 2018. Local protein sources in animal feed - Perceptions among arctic sheep farmers. J. Rural Stud. 59, 98–110. https://doi.org/10.1016/j.jrurstud.2018.02.004

Bell, M., 1981. Seaweed as a prehistoric resource, in: Brothwell, D., Dimbleby, G. (Eds.), Environmental Aspects of Coasts and Islands (BAR International Series 94). British Archaeological Reports (BAR), Oxford, England, pp. 117–126.

Blanz, M., Ascough, P., Mainland, I., Martin, P., Taggart, M.A., Dieterich, B., Wishart, J., Sayle, K.L., Raab, A., Feldmann, J., 2019. Seaweed fertilisation impacts the chemical and isotopic composition of barley: Implications for analyses of archaeological skeletal remains. J. Archaeol. Sci. 104, 34–44. https://doi.org/10.1016/j.jas.2019.02.003

Bogaard, A., Heaton, T.H.E., Poulton, P., Merbach, I., 2007. The impact of manuring on nitrogen isotope ratios in cereals: archaeological implications for reconstruction of diet and crop management practices. J. Archaeol. Sci. 34, 335–343. https://doi.org/10.1016/j.jas.2006.04.009

Bol, R., Eriksen, J., Smith, P., Garnett, M.H., Coleman, K., Christensen, B.T., 2005. The natural abundance of13C,15N,34S and14C in archived (1923-2000) plant and soil samples from the Askov long-term experiments on animal manure and mineral fertilizer. Rapid Commun. Mass Spectrom. 19, 3216–3226. https://doi.org/10.1002/rcm.2156

Britton, K., Müldner, G., Bell, M., 2008. Stable isotope evidence for salt-marsh grazing in the Bronze Age Severn Estuary, UK: implications for palaeodietary analysis at coastal sites. J. Archaeol. Sci. 35, 2111–2118. https://doi.org/10.1016/j.jas.2008.01.012

Bronk Ramsey, C., Higham, T.F.G., Brock, F., Baker, D., Ditchfield, P., 2009. Radiocarbon Dates from the Oxford AMS System: Archaeometry Datelist 33. Archaeometry 51, 323–349. https://doi.org/10.1111/arcm.12372

Bronk Ramsey, C., Higham, T.F.G., Owen, D.C., Pike, A.W.G., Hedges, R.E.M., 2002. Radiocarbon Dates from the Oxford AMS System: Archaeometry Datelist 31. Archaeometry 44, 1–149. https://doi.org/10.1111/arcm.12372

Brown, T.A., Nelson, D.E., Vogel, J.S., Southon, J.R., 1988. Improved Collagen Extraction by Modified

Longin Method. Radiocarbon 30, 171–177. https://doi.org/10.1017/s0033822200044118
Carlton, J.T., Hodder, J., 2003. Maritime mammals: terrestrial mammals as consumers in marine intertidal communities. Mar. Ecol. Prog. Ser. 256, 271–286.
Carvalho, M.C., Hayashizaki, K., Ogawa, H., 2008. Environment determines nitrogen content and stable isotope composition in the sporophyte of Undaria pinnatifida (Harvey) Suringar. J. Appl. Phycol. 20, 695–703. https://doi.org/10.1007/s10811-007-9271-7
Chapman, V.J., 1970. Seaweeds and their uses, 2nd ed. by Methuen and Co. Ltd., London.
Chimera, C., Coleman, M.C., Parkes, J.P., 1995. Diet of feral goats and feral pigs on Auckland Island, New Zealand. N. Z. J. Ecol. 19, 203–207.
Chisholm, B.S., Nelson, D.E., Schwarcz, H.P., 1982. Stable-Carbon Isotope Ratios as a Measure of Marine Versus Terrestrial Protein in Ancient Diets. Science (80-.). 216, 1131–1132. https://doi.org/10.1126/science.216.4550.1131
Clementz, M.T., Fox-Dobbs, K., Wheatley, P. V., Koch, P.L., Doak, D., 2009. Revisiting old bones: coupled carbon isotope analysis of bioapatite and collagen as an ecological and palaeoecological tool. Geol. J. 44, 605–620. https://doi.org/10.1002/gj
Codron, D., Clauss, M., Codron, J., Tütken, T., 2018. Within trophic level shifts in collagen–carbonate stable carbon isotope spacing are propagated by diet and digestive physiology in large mammal herbivores. Ecol. Evol. 8, 3983–3995. https://doi.org/10.1002/ece3.3786
Conradt, L., 2000. Use of a seaweed habitat by red deer (Cervus elaphus L .). J. Zool. Soc. London 250, 541–549.
Coplen, T.B., Kendall, C., Hopple, J., 1983. Comparison of stable isotope reference samples. Nature 302, 28–30.
Craine, J., Craine, J.M., Elmore, A.J., Aidar, M.P.M., Bustamante, M., Dawson, T.E., Hobbie, E. a, Kahmen, A., Mack, M.C., Mclauchlan, K.K., Michelsen, A., Nardoto, G.B., Pardo, L.H., 2009. Global patterns of foliar nitrogen isotopes and their relationships. New Phytol. 183, 980–992. https://doi.org/10.1111/j.1469-8137.2009.02917.x
Dockrill, S.J., Bond, J.M., Milles, A., Simpson, A., Ambers, J., 1994. Tofts Ness, Sanday, Orkney. An integrated study of buried Orcadian landscape. Whither Environ. Archaeol. 115–132.
Eide, M., Olsen, A., Ninnemann, U.S., Eldevik, T., 2017. A global estimate of the full oceanic 13C Suess effect since the preindustrial. Global Biogeochem. Cycles 31, 492–514. https://doi.org/10.1002/2016GB005472
Fenton, A., 1997. The Northern Isles: Orkney and Shetland. Tuckwell Press, East Linton.
Fogel, M.L., Tuross, N., Owsley, D.W., 1989. Nitrogen isotope tracers of human lactation in modern and archaeological populations. Annu. Rep. Dir. Geophys. Lab. Carnegie Inst. Washingt. 1988-1989 111–117.
Fraser, R.A., Bogaard, A., Heaton, T., Charles, M., Jones, G., Christensen, B.T., Halstead, P., Merbach, I., Poulton, P.R., Sparkes, D., Styring, A.K., 2011. Manuring and stable nitrogen isotope ratios in cereals and pulses: Towards a new archaeobotanical approach to the inference of land use and dietary practices. J. Archaeol. Sci. 38, 2790–2804. https://doi.org/10.1016/j.jas.2011.06.024
Froehle, A.W., Kellner, C.M., Schoeninger, M.J., 2010. FOCUS: Effect of diet and protein source on carbon stable isotope ratios in collagen: Follow up to Warinner and Tuross (2009). J. Archaeol. Sci. 37, 2662–2670. https://doi.org/10.1016/j.jas.2010.06.003
Furness, R.W., 1988. Predation on ground-nesting seabirds by island populations of red deer Cervus elaphus and sheep Ovis. J. Zool. 216, 565–573. https://doi.org/10.1111/j.1469-7998.1988.tb02451.x
Gaillard, C., Bhatti, H.S., Novoa-Garrido, M., Lind, V., Roleda, M.Y., Weisbjerg, M.R., 2018. Amino acid profiles of nine seaweed species and their in situ degradability in dairy cows. Anim. Feed Sci.

Technol. 241, 210–222. https://doi.org/10.1016/j.anifeedsci.2018.05.003
Gifford, T., 1879. Historical description of the Zetland Islands in the year 1733. Thomas George Stevenson, Edinburgh.
Gigleux, C., Richards, M.P., Curtis, N., Hutchison, M., Britton, K., 2017. Reconstructing diet at the Neolithic stalled cairn of the Knowe of Rowiegar, Rousay, Orkney, using stable isotope analysis. J. Archaeol. Sci. Reports 13, 272–280. https://doi.org/10.1016/j.jasrep.2017.03.048
Greenwood, Y., Orpin, C.G., Paterson, I.W., 1983. Digestibility of seaweeds in Orkney sheep. Proc. Physiol. Soc. 120.
Hall, S.J.G.G., 1975. Some recent observations on Orkney Sheep. Mamm. Rev. 5, 59–64. https://doi.org/10.1111/j.1365-2907.1975.tb00187.x
Hallsson, S. V., 1964. The uses of seaweeds in Iceland. IV Congr. Int. des Sigues Mar. 1961, Pergamon 398–405.
Hansen, B.B., Lorentzen, J.R., Welker, J.M., Varpe, Ø., Aanes, R., Beumer, L.T., Pedersen, Å.Ø., 2019. Reindeer turning maritime: Ice-locked tundra triggers changes in dietary niche utilization. Ecosphere 10. https://doi.org/10.1002/ecs2.2672
Hansen, H.R., Hector, B.L., Feldmann, J., 2003a. A qualitative and quantitative evaluation of the seaweed diet of North Ronaldsay sheep. Anim. Feed Sci. Technol. 105, 21–28. https://doi.org/10.1016/S0377-8401(03)00053-1
Hansen, H.R., Raab, A., Francesconi, K.A., Feldmann, J., 2003b. Metabolism of arsenic by sheep chronically exposed to arsenosugars as a normal part of their diet. 1. Quantitative intake, uptake, and excretion. Environ. Sci. Technol. 37, 845–851. https://doi.org/10.1021/es026074n
Heaton, T.H.E., 1987. The 15N/14N ratios of plants in South Africa and Namibia: relationship to climate and coastal/saline environments. Oecologia 74, 236–246.
Hedges, R.E.M., 2004. Isotopes and red herrings: comments on Milner et al. and Liden et al. Antiquity 78, 34.
Hewson, R., 1984. Scavenging and Predation Upon Sheep and Lambs in West Scotland. J. Appl. Ecol. 21, 843–868.
Houston, D., 1977. The Effect of Hooded Crows on Hill Sheep Farming in Argyll, Scotland: Hooded Crow Damage to Hill Sheep. J. Appl. Ecol. 14, 17–29.
Ingimundarson, J.H., 1995. Of sagas and sheep: Toward a historical anthropology of social change and production for market, subsistence and tribute in early Iceland (10th to the 13th century).
Jones, J.R., Mulville, J., 2016. Isotopic and zooarchaeological approaches towards understanding aquatic resource use in human economies and animal management in the prehistoric Scottish North Atlantic Islands. J. Archaeol. Sci. Reports 6, 665–677. https://doi.org/10.1016/j.jasrep.2015.08.019
Keeling, C.D., 1979. The Suess effect: ^{13}carbon-^{14}carbon interrelations. Environ. Int. 2, 229–300. https://doi.org/10.1016/0160-4120(79)90005-9
Kohn, M.J., 2010. Carbon isotope compositions of terrestrial C3 plants as indicators of (paleo)ecology and (paleo)climate. Proc. Natl. Acad. Sci. 107, 19691–19695. https://doi.org/10.1073/pnas.1004933107
Krueger, H.W., Sullivan, C.H., 1984. Models for carbon isotope fractionation between diet and bone. Stable Isot. Nutr. ACS Symp. Ser. No.258 205–220. https://doi.org/10.1021/bk-1984-0258.ch014
Landsborough, D., 1857. A popular history of British seaweeds. L. Reeve, London, Uk.
Lee-Thorp, J.A., Sealy, J.C., van der Merwe, N.J., 1989. Stable carbon isotope ratio differences between bone collagen and apatite, and their relationship to diet. J. Archaeol. Sci. 16, 585–599. https://doi.org/10.1016/0305-4403(89)90024-1
Lemesle, S., Erraud, A., Mussio, I., Rusig, A.M., Claquin, P., 2015. Dynamics of δ15N isotopic signatures

of different intertidal macroalgal species: Assessment of bioindicators of N sources in coastal areas. Mar. Pollut. Bull. 110, 470–483. https://doi.org/10.1016/j.marpolbul.2016.06.006
Martin, M., 1716. A description of the Western Islands of Scotland, 2nd ed. A. Bell, London, UK.
Matsubayashi, J., Tayasu, I., 2019. Collagen turnover and isotopic records in cortical bone. J. Archaeol. Sci. 106, 37–44. https://doi.org/10.1016/j.jas.2019.03.010
Mays, S., Beavan, N., 2012. An investigation of diet in early Anglo-Saxon England using carbon and nitrogen stable isotope analysis of human bone collagen. J. Archaeol. Sci. 39, 867–874. https://doi.org/10.1016/j.jas.2011.10.013
McCarroll, D., Gagen, M.H., Loader, N.J., Robertson, I., Anchukaitis, K.J., Los, S., Young, G.H.F., Jalkanen, R., Kirchhefer, A., Waterhouse, J.S., 2009. Correction of tree ring stable carbon isotope chronologies for changes in the carbon dioxide content of the atmosphere. Geochim. Cosmochim. Acta 73, 1539–1547. https://doi.org/10.1016/j.gca.2008.11.041
Moore, P.G., 2004. Burrowing on borrowed time: Tides in the affairs of the rabbit (Oryctolagus cuniculus). J. Nat. Hist. 38, 1315–1321. https://doi.org/10.1080/00222930310001552 32
Moore, P.G., 2002. Mammals in intertidal and maritime ecosystems: Interactions, impacts and implications. Oceanogr. Mar. Biol. Vol 40 40, 491–608.
O'Connell, T.C., Kneale, C.J., Tasevska, N., Kuhnle, G.G.C., 2012. The diet-body offset in human nitrogen isotopic values: A controlled dietary study. Am. J. Phys. Anthropol. 149, 426–434. https://doi.org/10.1002/ajpa.22140
O'Leary, M.H., 1988. Carbon Isotopes in Photosynthesis. Bioscience 38, 328–336.
Olsen, A., Omar, A.M., Bellerby, R.G.J., Johannessen, T., Ninnemann, U., Brown, K.R., Olsson, K.A., Olafsson, J., Nondal, G., Kivimäe, C., Kringstad, S., Neill, C., Olafsdottir, S., 2006. Magnitude and origin of the anthropogenic CO2 increase and 13C Suess effect in the Nordic seas since 1981. Global Biogeochem. Cycles 20, 1–12. https://doi.org/10.1029/2005GB002669
Orpin, C.G., Greenwood, Y., Hall, F.J., Paterson, I.W., 1985. The rumen microbiology of seaweed digestion in Orkney sheep. J. Appl. Bacteriol. 58, 585–596. https://doi.org/10.1111/j.1365-2672.1985.tb01715.x
Palsson, A., Girmsson, H., 1953. Demyelination in lambs from ewes which feed on seaweeds. Proc. Soc. Exp. Biol. 518–520.
Paterson, I.W., Coleman, C.D., 1982. Activity patterns of seaweed-eating sheep on North Ronaldsay, Orkney. Appl. Anim. Ethol. 8, 137–146. https://doi.org/10.1016/0304-3762(82)90139-0
Pellegrini, M., Snoeck, C., 2016. Comparing bioapatite carbonate pre-treatments for isotopic measurements: Part 2 - Impact on carbon and oxygen isotope compositions. Chem. Geol. 420, 88–96. https://doi.org/10.1016/j.chemgeo.2015.10.038
Raven, J.A., Johnston, A.M., Kübler, J.E., Korb, R., McInroy, S.G., Handley, L.L., Scrimgeour, C.M., Walker, D.I., 2002. Mechanistic interpretation of carbon isotope discrimination by marine macroalgae and seagrasses. Funct. Plant Biol. 29, 335–378. https://doi.org/10.1071/PP01201
Richards, M.P., Hedges, R.E.M., 1999. Stable Isotope Evidence for Similarities in the Types of Marine Foods Used by Late Mesolithic Humans at Sites Along the Atlantic Coast of Europe. J. Archaeol. Sci. 26, 717–722. https://doi.org/10.1006/jasc.1998.0387
Rose, M.D., Polis, G.A., 1998. The Distribution and Abundance of Coyotes : The Effects of Allochthonous Food Subsidies from the Sea. Ecology 79, 998–1007.
Ryder, M.L., 1983. Sheep and Man. Duckworth, London.
Schoeninger, M.J., DeNiro, M.J., Tauber, H., 1983. Stable Nitrogen Isotope Ratios of Bone Collagen Reflect Marine and Terrestrial Components of Prehistoric Human Diet. Science (80-.). 220, 1381–1383.
Schulting, R., Richards, M., 2009. Radiocarbon dates and stable isotope values on human remains, in:

Ritchie, A. (Ed.), On the Fringe of Neolithic Europe. Society of Antiquaries of Scotland, Edinburgh, pp. 66–74.

Schulting, R., Tresset, A., Dupont, C., 2004. From Harvesting the Sea to Stock Rearing Along the Atlantic Façade of North-West Europe. Environ. Archaeol. 9, 143–154. https://doi.org/10.1179/146141004790734478

Schulting, R.J., Vaiglova, P., Crozier, R., Reimer, P.J., 2017. Further isotopic evidence for seaweed-eating sheep from Neolithic Orkney. J. Archaeol. Sci. Reports 11, 463–470. https://doi.org/10.1016/j.jasrep.2016.12.017

Steel, T., 1975. The Life and Death of St. Kilda. Fontana, Glasgow.

Stephenson, W.A., 1968. Seaweed in Agriculture and Horticulture. Faber and Faber Limited, London.

Stevens, R.E., Lister, A.M., Hedges, R.E.M., 2006. Predicting diet, trophic level and palaeoecology from bone stable isotope analysis: A comparative study of five red deer populations. Oecologia 149, 12–21. https://doi.org/10.1007/s00442-006-0416-1

Styring, A.K., Fraser, R.A., Bogaard, A., Evershed, R.P., 2014. The effect of manuring on cereal and pulse amino acid δ15 N values. Phytochemistry 102, 40–45. https://doi.org/10.1016/j.phytochem.2014.02.001

Takahashi, Y., Matsumoto, E., Watanabe, Y.W., 2000. The distribution of δ13C in total dissolved inorganic carbon in the central North Pacific Ocean along 175°E and implications for anthropogenic CO2 penetration. Mar. Chem. 69, 237–251. https://doi.org/10.1016/S0304-4203(99)00108-5

Towsey, K., 2002. Orkney and the Sea: An oral history. Orkney Heritage, Kirkwall.

Virginia, R.A., Delwiche, C.C., 1982. Natural 15N abundance of presumed N2-fixing and non-N2-fixing plants from selected ecosystems. Oecologia 54, 317–325. https://doi.org/10.1007/BF00380000

Vogel, J., 1978. Isotopic assessment of the dietary habits of ungulates. S. Afr. J. Sci. 74, 298–301.

Webb, E.C., Lewis, J., Shain, A., Kastrisianaki-guyton, E., Honch, V., Stewart, A., Miller, B., Tarlton, J., Evershed, R.P., Webb, E.C., Lewis, J., Shain, A., Kastrisianaki-guyton, E., Honch, V., Stewart, A., Miller, B., Tarlton, J., Evershed, R.P., 2017. The influence of varying proportions of terrestrial and marine dietary protein on the stable carbon- isotope compositions of pig tissues from a controlled feeding experiment. STAR Sci. Technol. Archaeol. Res. 3, 28–44. https://doi.org/10.1080/20548923.2016.1275477

Webb, E.C., Stewart, A., Miller, B., Tarlton, J., Evershed, R.P., 2016. Age effects and the influence of varying proportions of terrestrial and marine dietary protein on the stable nitrogen-isotope compositions of pig bone collagen and soft tissues from a controlled feeding experiment. STAR Sci. Technol. Archaeol. Res. 2, 54–66. https://doi.org/10.1080/20548923.2016.1275477

Wolfhagen, J., 2019. Rethinking Human-Cattle Interactions at Çatalhöyük (Turkey) through Bayesian Analysis of Cattle Biometry and Behavior. Stony Brook, NY, Stony Brook University.

Zazzo, A., Balasse, M., Passey, B.H., Moloney, A.P., Monahan, F.J., Schmidt, O., 2010. The isotope record of short- and long-term dietary changes in sheep tooth enamel: Implications for quantitative reconstruction of paleodiets. Geochim. Cosmochim. Acta 74, 3571–3586. https://doi.org/10.1016/j.gca.2010.03.017